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The Organism-Centered Approach to Cultural Evolution

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Abstract In this paper, we distinguish two different approaches to cultural evolution. One approach is meme-centered, the other organism-centered. We argue that in situations in which the meme- and organism-centered approaches are competing alternatives, the organism-centered approach is in many ways superior. Furthermore, the organism-centered approach can go a long way toward understanding the evolution of institutions. Although the organism-centered approach is preferable for a broad class of situations, we do leave room for super-organismic (group based) or sub-organismic (meme-based) explanations of some cultural phenomena.

Keywords Cultural evolution · Memetics · Institutions

1 Introduction

The naturalistic study of culture and institutions often builds upon tools and methods developed in evolutionary biology (Hodgson 1993; Henrich 2006). Those who follow this route all seem to accept that cultural evolution differs in at least some respects from biological evolution, although the nature of these differences and their relative importance for the study of cultural evolution has been the object of intense debate among scientists and philosophers (see Aunger 2000; Dennett 1995; Jablonka and Lamb 2005; Lewens 2012; Mesoudi et al. 2006).

A number of different evolutionary approaches to culture can be distinguished, but one central divide is between those approaches that center on replicators (or memes) and those that center on organisms (The meme/replicator-centered approach we will abbreviate as MC, whereas the organism-centered approach will be abbreviated as OC.). In this paper, we want to argue for the superiority of the OC over the MC. We will argue that the MC leads to a number of problems, and that these problems do not arise for an OC. This argument entails that the meme and organism-based views are not mere terminological variants, as some have argued or assumed (Wimsatt 1999; Henrich et al. 2008). Instead, they have substantive differences, and it is the OC that is generally superior.

In Sect. 2 we will sketch the organism- and meme-centered approaches. Section 3 deals with the benefits of adopting the OC. In Sect. 4, we discuss some challenges to that approach and show why these challenges do not pose any real problems, or pose fewer problems for this approach than for the MC. Section 5 extends the OC to institutions. We conclude with a discussion of the broader implications of our arguments for the evolutionary study of culture and organizations.

2 Distinguishing the Organism- and Meme-Centered Approaches

In *The Selfish Gene*, Richard Dawkins defended what he would later call 'universal Darwinism'. Universal Darwinism is the idea that whenever there are replicators, variation, and differential survival, evolution will occur, be it on this planet or on another. But there is also some

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evidence on this planet, according to Dawkins, that the evolutionary algorithm can run on substrates other than genes—the (main) replicating units in biological evolution:

> The gene, the DNA molecule, happens to be the replicating entity that prevails on our own planet. There may be others. If there are, provided certain other conditions are met, they will almost inevitably tend to become the basis for an evolutionary process. But do we have to go to distant worlds to find other kinds of replicator and other, consequent kinds of evolution? I think that a new kind of replicator has recently emerged on this very planet. It is staring us in the face. It is still in its infancy, still drifting clumsily about in its primeval soup, but already it is achieving evolutionary change at a rate that leaves the old gene panting far behind.
> The new soup is the soup of human culture. (Dawkins 1976, 206–207)

In the subsequent lines, Dawkins famously proposed to use the noun 'meme' for this cultural replicator.

Since Dawkins first proposed the new field of memetics, others have elaborated his ideas. Although the meme idea never gained a lot of traction among scientists, some scientists did attempt to develop meme-theory into a set of viable explanations for cultural phenomena. For example, biological anthropologist Bill Durham (1991) and archaeologist Stephen Shennan (2002) have both produced memetic accounts of cultural traditions. Philosopher Daniel Dennett (1991, 1995) and psychologist Susan Blackmore (1999) focus more on conceptual issues. They try to answer questions like what memes are and how they spread. In their writings, the conceptual concerns are mixed with an unwavering belief in the potential of a meme-centered approach to human thinking and culture.

Memeticists, of course, defend meme-centrism, a view with two central tenets. The first tenet is that the evolutionary study of culture needs to track the fate of memes—their mutations and changes in relative frequency. Blackmore (1999), for example, understands cultural fitness in the following way: "what is fitness for a short melody? It is the ability to survive and reproduce, which in terms of music means being copied, stored and reproduced more frequently than other melodies" (260). For the MC, what ultimately matters is the number of copies of the meme that end up in the meme pool. And this meme pool is not restricted to the heads of humans—they can find their home in a wide array of human artifacts, most obviously in written words, but also in all varieties of objects, from pieces of clothing to the utensils we use. For the MC, such memes reside in a utensil such as a fork, and changes in the relative frequency in alternate types of forks (two tined, three tined, four tined, etc.) are understood in terms of competition among the meme for two tines, the meme for three tines, etc. And new kinds of utensils, like the spork, could be understood as a result of a single object being the result of two memes, one for a fork and another for a spoon—a kind of memetic chimera.

The second central tenet of meme-centrism is that memes use organisms to propagate their own interests. Many characteristics of the meme are explained by the contribution of those characteristics to the successful replication of the meme. In a way, memes are using our bodies and brains to maximize their fitness. Memes are replicators that use our brains as their vehicles to replicate themselves; hence, the ultimate beneficiaries of cultural evolution are memes (Blackmore 1999). Much in the way that other animals seem to behave as if they are primarily interested in getting as much of their genes to the next generation, cultural organisms like humans often behave as if they are primarily interested in getting their ideas to the next generation (or the next village), even if they have to bear considerable costs in order to increase the frequency of these ideas. According to Dawkins and other memeticists, cultural traits spread not because they are useful for the individuals with these traits, but mainly (and often even solely) because they aid meme propagation (Laland and Brown 2002). Dennett and Blackmore even suggest that brains are in part designed by memes to get passed on (Dennett 1991; Blackmore 1999). For those who take the meme's eye view, the prototypical meme is the chain letter: a chain letter promises punishment for those who don't distribute it further (or reward for those who do) and hence influences events such that it gets replicated over and over (Brodie 1996; Goodenough and Dawkins 1994).

These two MC tenets can be set against an OC view of cultural evolution. In contrast to the first MC tenet, the OC takes the organism and the cultural traits they adopt to be the locus of cultural evolutionary theory. Like the MC, the OC is concerned to understand the spread and impact of cultural traits, but radically differs with respect to the question of what counts as an instance of replication. For the OC, replication occurs when a naïve individual adopts a cultural variant, whereas for the MC, replication can occur in the absence of organisms adopting the variant. For example, if an idea occurs to me and I write it on a doc on my computer, which is then backed up, how much replication has occurred for the idea? The MC holds that it has replicated at least twice: It replicated when I wrote it down (it was once only in my head, but is now in my head and in the computer), and again when the hard drive was backed up. We said *at least* twice since for the MC there could be many more instances of replication in this scenario. The meme could be replicating within my brain, it could replicate when it is opened and thus loaded into RAM, etc. By contrast to the MC, the OC counts only one cultural

variant per biological organism. I can create, adopt, and modify cultural variants, but in order for a cultural variant of mine to be replicated, it must be adopted by another person. It is not enough for my ideas to be written down, typed up, or in any other way recorded. The OC, then, treats culture not unlike we treat genes when tracking genetic evolution. When an organism grows, the number of copies of its genes increases, and it is constantly shedding copies of its genes in skin cells, hair, etc. Despite these gains and losses of gene copies, when a biologist asks the question of whether evolution has occurred, she does not count total copies of genes. Evolution is standardly defined as generational change in gene frequency, but it is not actually gene frequency that is counted. Instead, it is gene frequency *per organism* that is counted, i.e., each gene is counted only once per organism. For an organism to double the population-level tally of one of its genes, it does not suffice to grow twice as massive, it must instead produce an offspring. We think that this is the right approach for the biological cases, and for similar reasons the OC is the right one for culture. The MC, then, is making the mistake that a biologist would make were they to count within-organism cellular growth as reproduction, and thus as a basis of genetic evolution.

The second tenet of the OC differs from that of the MC, though not as radically as the first tenet. Like the MC, the OC allows for cultural variants to win evolutionary competitions even though organisms or groups of organisms reduce their fitness by adopting these winning variants. But the OC focuses less on the maladaptive effects that culture can have for cultural organisms. Instead, the focus is on how cultural evolution can increase the fit between cultural organisms and the environment in which they live. This accords with the argument made by Ramsey (2007) that for a cultural capacity to be an adaptation, a purely parasitic/viral/memetic view of culture is untenable. And if, as seems highly probable, the cultural capacities of humans are adaptations, then memes are unlikely to merely be operating for their own ends, parasitizing and controlling their hosts. The MC does however have ways to account for memes at times being adaptive. According to Blackmore, for example, "a lot of memes may actually thrive precisely because they do contribute to genetic fitness, but that contributing to fitness is only one of many ways in which a meme can be replicated" (as cited in Laland and Brown 2002, 205–206). Yet, on the side of those who take the OC, this difference in emphasis does entail a strong interest in the evolution and the adaptive value of cultural capacities, and in the co-evolution of genes and culture.

It is clear that the MC and OC are distinct and differ in fundamental ways, especially when considering whether replication has taken place. Let's now consider the advantages of the OC.

3 The Advantages of the Organism-Centered Approach

Both philosophers and scientists have criticized the MC. One recurring criticism is that memes as gene-like discrete entities probably do not exist, or that if the do exist, they represent a special case—not a general account—of culture (Sperber 2000; Midgley 2000). Other criticisms focus on the memeticist's insistence that replicators are necessary for cultural evolution, arguing that cumulative adaptive evolution can occur even in the absence of replicators (Boyd and Richerson 2000). In our view, both criticisms have been successfully sidestepped by memeticists by pointing out that the bulk of what has been done under the flag of memetics never rested on these—indeed questionable—assumptions (O'Brien et al. 2010). Even if these charges against the MC are not fatal, however, we will argue here that the OC offers considerable and real advantages over the MC. The advantages are both epistemic and conceptual.

Consider first the conceptual advantages. Evolution by natural selection, as originally articulated by Darwin (1859), centers on three key conditions: there must be variation, at least some of this variation must be heritable, and at least some of the heritable variation must bring about differences in fitness. The MC must therefore have an account of what meme variation, heritability, and fitness consist in. And because fitness is about reproductive success, there must be clear criteria for what counts as an instance of reproduction.

What is reproduction for the MC? Instead of offering a set of criteria, we will pose several questions that need to be answered in order for there to be a coherent MC. First, can there be multiple copies of a meme within an individual's head? If so, how are neuronal states individuated into distinct memes? Second, how are memes to be individuated within artifacts? In the computer case from the previous section, what facts determine how many copies of a meme there are on a computer? If a file is duplicated, is the meme duplicated? What if the duplicated file is subsequently deleted, but when this occurs it is not actually expunged, but part of the hard drive is flagged as an area that can in the future be overwritten? And for the spork example above, is this a case of fork and spoon memes reproducing and finding themselves within the same utensil, instead of each occupying distinct utensils? Or is a spork a unique meme related to spoon and fork memes, but not an instance of either? These are just some of the sorts of questions that a MC needs to answer, and even meme enthusiasts like Dennett admit that these answers are difficult to come by for the MC: "There are vexatious problems about just what the boundaries of a meme are—is wearing a baseball cap backward one meme or two (wearing a cap, and putting it on backward)?" (Dennett 2006, 81).

By contrast to the MC, the OC counts only one variant per person. Thus, no criteria for intra-cranial reproduction need be developed, nor does one need to operationalize reproduction within artifacts. Cultural reproduction is therefore not based on such things as the number of copies of a file on a hard drive. We are not here claiming that the number of copies of the file is *independent* of cultural fitness, only that reproduction is not *defined* in terms of such duplication. It might be that having many copies of a file helps a person retain a particular variant and can thus boost fitness. But whether fitness is boosted is an empirical matter, not one based on the very definition of reproduction.

We do not mean to imply that the OC does not have difficult conceptual problems to solve. Instead, one central concept that the OC needs to clarify is the notion of adopting a variant. When should we count an individual as having adopted a variant? We recognize this as a challenging question and will turn to it in the following section. Our point is thus not to argue that only the MC faces difficult conceptual puzzles, but rather that the ones that it faces are much more challenging than those of the OC.

Now consider the epistemic or practical advantages of the OC for a science of cultural evolution that wants to explain and predict cultural changes. Many of the advantages are tied directly to the conceptual issues just mentioned. In order to measure cultural fitness for the OC, we merely need to track which individuals have adopted the variant, we don't need to burrow into their brains to see how many meme copies there are between their ears. And we need not conduct sophisticated analyses like in the above computer example in order to tell how many copies of a particular meme reside within.

It is not merely that the OC is conceptually and empirically less burdensome, it is also that it focuses on the entities that are most central to the explanatory and other scientific interests of the humanities and the social sciences. If cultural evolutionists would embrace the MC and focus on the number of memes (e.g. the number of produced sporks), irrespective of whether these memes are actually adopted by humans, then this would decrease the relevance of cultural evolution for the social sciences and the humanities. After all, these disciplines are mainly—if not solely—interested in culture inasmuch as culture affects the behavior and thinking of human beings.

4 Challenges to the OC

In the previous section, we mentioned a challenge to the OC: If the OC says that what counts in cultural evolution is the adoption of a cultural variant, then what are the criteria for adoption? In some cases, this is rather straightforward. For instance, individual J has adopted the cultural variant *spork* when J uses sporks to eat. Likewise, individual J* has not adopted *spork* when J* does not use sporks, and has never even heard of sporks. Yet, many cases are less straightforward. Take for instance someone who heard 5 years ago that sporks would become the cutlery of the future, but has never used a spork himself. In fact, for the last 4 years, he didn't spend any thoughts on sporks. Has this person adopted the spork variant when he first heard about the existence of sporks? Did the adoption of the spork variant stop when he stopped thinking about it?

To answer questions like these, we need a criterion for what counts as the adoption of a variant in cultural evolution. It might seem ideal to draw this criterion from a similar one used in evolutionary biology. Yet, the large differences between cultural evolution and biological evolution probably thwart the straightforward copying of a biological criterion and/or its operationalization in cultural evolution. Nevertheless, let's begin with a sketch of the criterion for adoption in biological evolution and then spell out why and how this criterion (or its operationalization) needs to be fine-tuned to fit the case of cultural evolution.

In biological evolution, the question of whether an individual possesses a variant is relatively straightforward, especially if the variant in question is an allele. Although complications like the genetic background of the allele (which other gene variants the individual possesses) matters for its expression, it is nevertheless true that an individual either possesses the allele or does not—there are not difficult intermediary cases. That said, evolutionary biologists are often chiefly interested in the evolution of phenotypic traits, not merely the underlying genes. This can complicate matters since phenotypic variants can rarely be simply mapped onto genetic variants: Large genetic variation can result in little or no phenotypic variation, and there are also cases where small genetic differences makes for huge phenotypic differences (cf. phenotypic plasticity). Moreover, the genetic system controlling the phenotypic variants is often poorly understood, especially for the behavioral traits.

Evolutionary biologists have come up with solutions to tackle these problems. First, it is common among evolutionary biologists to abstract away from the details of the genetic system that controls the traits. This solution is difficult to apply in the cultural realm because abstracting away from the details of the heredity system is fine as long as one can safely assume that there is a heredity system underlying the trait(s) and that there is a more or less clear distinction between the heredity system and the observable expressions of the hereditary information. The genotype-phenotype distinction is a clear distinction, and it is absolutely crucial for understanding biological evolution. Yet no such generally accepted and clear distinction exists between the coding and the coded variants is available for

cultural evolution. As Laland and Brown (2002, 207) note, "[m]uch debate and confusion has centred around what, in meme terms, is analogous to the genotype-phenotype distinction between the genetic constitution of an organism (its genotype) and the characteristics of the organism itself (its phenotype)." The debate and the confusion are not limited to the memetic school within cultural evolution, but are also present in the OC.

Furthermore, while it is true that an individual often clearly either possesses or does not possess a biological variant, with culture there is considerably more vagueness concerning the possession of cultural variants. Has the person "adopted" the idea of a spork when that person learned about the existence of sporks in 2007, even if she hasn't used it since and would have great difficulty even drawing a spork? And what should cultural evolutionists do with the following degrees of adoption: person A knows what a spork is, talks a lot about sporks, but never uses them, person B knows what a spork is, uses them regularly, but cannot draw a spork, and person C knows what sporks are, never uses them, but makes sporks for other people? All three of them seem to have adopted the cultural variant, but each of them in different ways and to different degrees.

We think that the differences between the biological and the cultural cases we mentioned are—at least to some extent—real. Yet they do not lead to insurmountable difficulties. Many of the difficulties can be addressed by simply providing a solid definition of culture. This definition of culture will also prove useful to address the second problem, because it implicitly harbors a conception of what the adoption of a cultural trait amounts to. We will use the conception of culture offered by Ramsey (2013), since his account represents the most recent and thorough treatment of the concept of culture. Ramsey defines culture in the following way: "Culture is information transmitted between individuals or groups, where this information flows through and brings about the reproduction of, and a lasting change in, the behavioral trait" (466). All of the details of this complex definition need not concern us here, but what is of central importance is his criterion that in order for information to be culture, it must bring about the reproduction of a behavioral trait. Thus while much information can be passed on from individual to individual, only a subset is culture. Genetic information that is passed on between individuals is not culture, but neither is what Richerson and Boyd (1997) call communication, i.e. ephemeral information that has no long-term impact on the phenotype.

This criterion provides us with a constraint on what counts as "adopting a cultural variant"—it must be culture as defined by Ramsey, i.e., it must play a role in reproducing behavior. Merely being influenced by a cultural variant is not enough. If I see that my peers are wearing skinny jeans and this causes me to feel bad about wearing my baggy jeans, information about the skinny jean cultural variant has been received by me, and it has changed my behavior (making me a bit more self conscious, for example). Despite this information flow and behavioral change, however, it is not the case that the skinny jean cultural variant has been adopted by me. For that to happen, the information about skinny jeans must have flowed to me through imitation or social learning and prompted me to purchase and wear skinny jeans.

One might object that just knowing about skinny jeans on others should count as cultural flow. Our reply to this is that if a person is a cultural evolutionary dead end—if the information is not going to engender behavioral reproduction—then it should not count as adopting a cultural variant. This parallels the case of biological evolution: Biological fitness is not merely based on the propensity of producing offspring, but is instead based on the production of offspring capable of producing offspring themselves. An individual that merely produces sterile offspring (a *Drosophila* with the grandchildless gene, for example) is not more biologically fit than another individual who produces no offspring. Thus just as our concept of fitness-relevant cultural reproduction requires cultural offspring capable of creating offspring themselves, so biological offspring must be viable and fertile in order for them to have evolutionary significance.

We therefore have a criterion for what counts as adopting a cultural variant. This helps lay the foundation for an organism-based account of cultural evolution. This criterion for adoption is especially important for qualitative traits, but also helps with quantitative traits. We should note, however, that in the biological case, the evolution of quantitative traits does not necessarily need a clear boundary between possessing a trait and lacking a trait. How venomous members of a snake species are may vary on a continuum from no venom to highly venomous. In such a case, it may not make sense to divide the population into venomous and non-venomous. Instead, for the sake of tracking the evolution of the degree of venomousness, the mean level of venomousness could be recorded in the absence of clearly defined boundaries.

Similar cases can occur for humans. One could record particular scalar properties of jeans—the size of the pant-leg opening, for example—to track their cultural evolution. A persistent reduction in pant-leg opening size over time is evidence that skinniness is being selected for in jeans. And it is evidence of cultural flow in the Ramsey sense. Thus, the OC works for quantitative traits just as it does for qualitative traits. The crucial difference between the MC and OC for this example is that while the OC records the jeans that people are wearing, the MC would record the jeans that people have in their closets (whether or not they wear them), in stores (whether or not they are successfully

being sold), and all other representations of jeans. This again points to both the massive epistemic advantage of the OC, but also its connection to the main cultural explanandum: why people wear the kind of jeans they do, and how and why jean fashion changes over time.

It is a clear practical advantage to only have to count the number of individual organisms that have adopted cultural variants, and not disembodied memes as well. In addition to this clear advantage, because the OC closely aligns with how biologists count gene frequency changes in populations (counting only one allele per organism), many of the methods that biologists have developed for biological evolution can readily be adopted by this account of cultural evolution. For example, instead of needing to follow the fate of all individuals in studying cultural selection, a wide variety of alternative methods can be used. In fact, most of the ten methods that Endler (1986) listed for detecting natural selection in the wild can be translated quite straightforwardly to detect cultural selection, e.g., the study of correlations of cultural traits with environmental factors (method I) and cohort analysis (method VII). Moreover, experimental studies are equally possible.

The OC, then, has clear advantages over the MC, but it has not been shown that the OC is the only account that one needs. The hierarchical account of natural selection (e.g., Brandon 1990) sees organismic selection as the most important form of selection in evolution, but not the only one. Let's now consider selection above and below the level of the organism.

5 Cultural Evolution and Institutions

We have seen that the OC is usually superior to the MC for both conceptual and epistemic reasons. The OC is the best account for the vast majority of cases, even though there might be cultural phenomena for which the MC is superior (Sterelny 2006). Our argument is thus not that the OC is always superior to the MC, or that it is the only model of culture that one will ever need, but that for the majority of cases, the OC is both conceptually and empirically superior. This account therefore does not preclude some sort of multi-level selection for culture: Note that Ramsey's definition of culture understands culture as "information transmitted between individuals or groups"—thus he recognized that sometimes one might need to go up to a group or institutional level in order to fully capture cultural dynamics. Just as in the case of biological evolution, where there can be higher-level properties of groups that are not contained in any individual—sex ratio, for example—so there can be cultural traits that have not been adopted by any individual, but have nevertheless been adopted by a group. For example, mask making as a craft can be adopted by a group of individuals while none of the individuals of the group masters the craft in whole.

We propose that when one addresses questions about the cultural evolution of institutions, that one first attempt to use the OC and move on to higher-level (or lower-level) accounts only when the OC is clearly inadequate. This approach is a return to the framework offered by Darwin (1859) in the *Origin*: Organismic selection is the primary engine of adaptive change in evolution. But there are cases in which going up a level seems necessary, especially when there are new properties that exist only at the group level. For Darwin in his (1871) *Decent of Man*, proportion of altruists was just such a property. An individual cannot bear the property of having a particular proportion of altruists, but groups can. And if there can be group-level selection for this property, then there can be an evolutionary response to selection at this level.

In addition to going up a level, there are cases of biological evolution that are best understood as operating at the sub-organismic, genic level. Meiotic drive is one such example—this is a case in which particular alleles cheat the meiotic lottery and get their copies into the next generation at a disproportionately high frequency. Such cases, like the mouse *t* haplotype, can become common in a population in spite of being bad for the individuals bearing the allele (Morita et al. 1992). When situations like this occur in cultural evolution, it is prudent to resort to a meme-centered approach. But just as such situations are not the dominant evolutionary force in organisms, so, we suspect, meme selection is not the dominant force in human cultural evolution (though this is, ultimately, an empirical matter). If this is true, then for the vast majority of cases, the OC will be the best approach to cultural evolution.

Of course, sometimes cultural traits may spread because they really are viruses of the mind. In those cases, the "beneficiary" of the cultural evolution process is the cultural variant, and not the individuals who adopt the variant. The cultural variant is the beneficiary of the selection process if the selection process results in adaptations on the level of the cultural variant (Eldredge 1985). Jokes, for example, often tend to become funnier and easier to memorize (Loewenstein and Heath 2009). Quite likely, these properties are adaptations of the joke to human cognition and communication. This is the version of the meme's eye approach that can sometimes be fruitful for understanding cultural evolutionary dynamics. But even in cases where this kind of MC makes sense, it is important to see that the memes need to be adopted by individuals in order to be relevant for cultural evolution.

Nowadays, cultural evolution theories are often used to make sense of institutions, both in scientific study of institutions and in the philosophical enterprise of social ontology. At what level do we need to tackle the evolution of

institutions? Can we get a grip on the evolution of institutions at an organismic level, or does this require higher (or lower) level selection?

First of all, what does the cultural evolution of institutions even mean? And what insight might it offer? If evolution involves changes in the frequency of types, or in the displacement the mean value of traits, then there have to be multiple entities that we can track over time. One possibility is that we wish to understand the differential success of competing companies or other institutions, e.g. Burger King versus McDonald's. The success of these companies might be evaluated in a number of ways, such as how much revenue is generated for their shareholders, how many franchises they have, how many meals they serve. No one measure is the uniquely correct one, they are just answering different questions for different ends. But if we are interested in what the cultural impact of these competitors is, we are apt to focus on individual humans, and in particular how many individuals adopt the Burger King versus McDonalds variants, that is, how many repeatedly eat at either chain. And if one takes this approach, one is clearly employing the OC.

If instead the object of study is not the differential adoption of competing brands, but instead the change in a single institution (type or token) over time, then we should first ask whether this is even a case of cultural evolution. At one scale of analysis (the entire institution), the change might be better analogized with biological development, not evolution. For instance, institutions sometimes take on new functions and lose others. While cultural evolutionary theories have seen these changes as evolutionary changes (Hodgson 2004), such changes seem to better resemble developmental changes in biological organisms than evolutionary changes in trait frequencies over time. But even if this is merely a case of development at this higher level of analysis, it does not mean that the changes cannot be understood in terms of cultural evolution—it is just that the evolution is apt to be occurring at a lower level. One potentially fruitful level of analysis is the organism, studying which variants (which institutional practices, say) are adopted (by whom and why) and how this changes over time—and such a level of analysis is clearly in accord with the OC. This may even help to understand the emergence of new institutions and the changes in functions of existing institutions. For example, over the last two decades, libraries have assumed new functions. Before 2000, most university libraries collected information resources and made these available for students and staff. After 2000, more and more university libraries assumed the function of stimulating collaborative study. In part, this switch in function occurred because the libraries decided to redesign their physical spaces. But even though the supply of new spaces played a role in this change, it was the behavior of the users that made the change in function robust (Bryant et al. 2009).

6 Conclusions

In this paper, we have shown that the OC is superior to the MC in many respects. Although the MC's focus on the meme pool and the fate of memes superficially resembles fruitful approaches in evolutionary biology, it obscures more interesting parallels between cultural and biological evolution. For instance, the MC seems to forget or ignore that population geneticists do not count the number of genes in a population, but count only one gene for each organism in the population. The OC avoids these problems, while at the same time makes the evolutionary study of culture more manageable and more germane to core cultural explananda. Yet, the OC is not without its own challenges. Most importantly, the OC needs to answer questions about how cultural evolutionists can determine whether an organism has adopted a cultural variant. We argued that these problems are not endemic to cultural evolution, but also occur in biological evolution. In fact, evolutionary biologists have found ways of dealing with these problems, and their solutions are readily applicable to cultural evolution.

Despite our heavy criticism of the MC, we don't think that this is—or should be—interpreted as the deathblow to memetics. There is some evidence that memes have a useful explanatory domain, and attempts to revive memetics as a quite specific approach to cultural evolution are worth consideration. Kim Sterelny, for example, has defended a place for a meme-based approach to cultural evolution, alongside other approaches. He writes: "As I see it, the crucial element of a meme-based theory is that the fitness of the memes themselves plays a crucial explanatory role." (Sterelny 2006, 155). Yet he implicitly interprets the fitness of the meme as the likelihood that the meme is adopted by an individual and not as the likelihood that the meme is copied. Hence, although Sterelny sees a place for an explanation of cultural evolution at the lower, 'meme'-level, his 'revived memetics' is perfectly reconciliable with the central tenets of the OC.

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